Epipedobates simulans, a New Cryptic Species of Poison Frog from Southeastern Peru, with Notes on E. macero and E. petersi (Dendrobatidae)

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ASTRACT

Epipedobates simulans is a new species of dendrobatid poison frog from humid forest at the base of the eastern Andes (400–600 m elev.) in the upper Madre de Dios drainage of southeastern Peru. It is very similar to Epipedobates petersi (Silverstone), a composite species that included specimens of E. simulans in the type series. Although similar in color and morphology, these species have allopatric distributions and very different vocalizations.

The advertisement call of Epipedobates petersi is shown to be extraordinarily variable. The call may be produced in trains of single, double, or triple notes, with occasional groups of four notes, all at a frequency below 4000 Hz. The call of Epipedobates simulans is a continuous train of single, well-spaced notes given above or mostly above 4000 Hz.

Epipedobates simulans is geographically closer to E. macero Rodríguez and Myers, which also has been confused with E. petersi. The range of E. macero is extended northward from the Río Madre de Dios basin to the upper Río Purús near the Brazilian border.

RESUMEN

Epipedobates simulans, especie nueva, es un dendrobátido venenoso del bosque húmedo al pie de los Andes orientales (altitud 400–600 m) en el cuenca alta del río Madre de Dios, al sudeste del Perú. Es muy similar a Epipedobates petersi (Silverstone), una especie compuesta que incluyó

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ejemplares de *E. simulans* en la serie tipo. Aunque similares en coloración y morfología, estas especies tienen distribuciones alopátricas y cantos muy diferentes.

Se demuestra que el canto de llamado de *Epipedobates petersi* es extraordinariamente variable. El canto consta de series de notas individuales, dobles, o triples, con grupos ocasionales de cuatro notas, todas en una frecuencia menor a 4000 Hz. El canto de *Epipedobates simulans* es un tren continuo de notas individuales que están bien separadas y que exceden, al menos en su mayor parte, los 4000 Hz.

Epipedobates simulans es más cercano geográficamente a *E. macero* Rodríguez y Myers, que también ha sido confundido con *E. petersi*. Se extiende la distribución geográfica de *E. macero* desde la cuenca del río Madre de Dios hacia al norte, hasta el río Alto Purús cerca a la frontera con Brasil.

INTRODUCTION

The genus *Epipedobates* comprises a few dozen relatively primitive poison frogs (Myers, 1987). About half the currently recognized species occupy distributions close to the Andean front along the western edge of Amazonia—from southern Colombia to northern Bolivia. These are mostly restricted ranges, although one Peruvian species, *Epipedobates petersi*, was conceived by its describer as having a north-south distribution of about 1000 km (Silverstone, 1976: 19 [map], 37–38).

Rodríguez and Myers (1993: 13) recently implied that the geographic range of *Epipedobates petersi* should be shorter by several hundred km. Three of the original paratypes of *petersi* are southern outliers that were thought to represent an unnamed population of smaller frogs having "most of the characteristics of northern *petersi*." Additional specimens and tape recordings from the southern population allow us to diagnose this cryptic species with reasonable confidence.

***Epipedobates simulans*, new species**
Figures 1A–D, 2–9

Phyllobates petersi Silverstone, 1976: 37 (part: the three British Museum paratypes from La Unión, Río Huacamayo, Puno).
Epipedobates sp., Rodríguez and Myers, 1993: 13 (in footnote). Rodríguez and Emmons, 1994: 150.

HOLOTYPE: MUSM 16996 (field no. LR 5953), an adult female collected on June 1, 1992, by Lily O. Rodríguez, on ridge along Río Távara [trib. Río Tambopata] just below confluence of Río Candamo and Río Huaca-

mayo,[4] about 450 m elev. (13°31'S, 69°41'W), Depto. Puno, Peru. The type locality is in the Zona Reservada Tambopata-Candamo.[5]

PARATYPES: A total of 12 adults, all from Peru, as follows: AMNH 155164, same locality as holotype except at 550 m elev., Depto. Puno (L. O. Rodríguez, June 3, 1992). AMNH 155165, 155166, Atalaya, 600 m, near junction of Río Carbón with Río Alto Madre de Dios (12°59'S, 71°10'W), Depto. Cusco (L. O. Rodríguez, J. Icochea, and Ariadne Angulo, August 28, 1993). BMNH 1907.5.7.9–1907.5.7.11, La Unión [nr. confluence Río Huacamayo and Río La Pampa, ca. 300 m, 13°32'S, 69°38'W, Depto. Puno]; collected by G. Ockenden prior to 1907. MUSM 15503–15505, 16936–16938, Río Távara, Prov. Carabaya, Depto. Puno (José Moscos and Fonchii Chang, August 15–18, 1992, and J. Icochea, August 17–21, 1996).

ETYMOLOGY: The species name *simulans* (resembling) is the present participle of the

Latin verb *simulo* (to make like or to assume the appearance of anything)—in allusion to the resemblance of this species to one with which it has been taxonomically confused.

DEFINITION AND DIAGNOSIS: A small to medium-size dendrobatid with an adult snout-to-vent length (SVL) of about 19–27 mm. Head and back blackish with bronzy brown highlighting, strongly granular; sides black, with a bright yellow stripe extending obliquely from groin to tip of snout; pale labial stripe from near naris to base of upper arm; a pale spot on anterodorsal base of thigh; ventral surfaces blue with black reticulum. Lacking concealed axillary and groin or calf spots. Teeth present on maxillary arch. Appressed first finger about equal to second; finger discs weakly to moderately expanded; third finger disc of adults about 1.2–1.8 times wider than finger; third finger sexually dimorphic, wider in males. Toes without webbing. Vocalization a long train of well-spaced (ca. 2/sec), short ($\leq$ 0.1 sec), frequency-modulated peeps in a range of about 3800 to 4500 Hz; terrestrial.

Epipedobates simulans is a member of the *E. petersi* species group (sensu Schulte, 1989). It appears nearly identical to *E. petersi* but differs in smaller average size, a darker (blackish vs. brown) dorsum, and especially in vocalization (see Comparisons with *E. petersi*); these two are widely separated geographically. *E. simulans* approaches the range of *E. macero* (Rodríguez and Myers), which is a larger frog easily distinguished by its red dorsum, incomplete lateral stripe, and vocalization. The more southern *E. bolivianus* (Boulenger) is about the same size as *E. simulans*, but the anterior and posterior thighs are conspicuously marbled in *bolivianus* (Rodríguez and Myers, 1993: fig. 10).

MEASUREMENTS OF HOLOTYPE (in mm): The holotype, dissected high along the right side, is an adult female containing large ova. Length from snout to vent 27.0; tibia length between heel and outer surface of flexed knee 12.0; greatest width of body 11.4; head width between angles of jaws, and between outer edges upper eyelids, 7.7 and 7.5, respectively; approximate width of interorbital area 2.8; head length (sagittal) from tip of snout to angle of jaw 7.0; tip of snout to center of naris (sagittal) 0.7; center of naris to anterior edge of eye 2.4; distance between centers of nares 3.2; eye length from anterior to posterior edge 3.3; horizontal diameter of tympanum about 1.9; corner of mouth to lower edge of tympanic ring 0.7; hand length from proximal edge of large medial palmar tubercle to tip of longest (third) finger 6.4; width of disc of third finger (and width of penultimate phalanx below disc) 0.8 (0.5); width of discs (and penultimate phalanges below discs) of third and fourth toes both 1.0 (0.5).

DESCRIPTION OF TYPE SERIES

EXTERNAL MORPHOLOGY: A small to medium-size dendrobatid, with adult males attaining about 23 mm SVL and adult females about 27 mm SVL (measurements and proportions summarized in table 1). Dorsal skin of head, body, and hind limbs coarsely and conspicuously granular; skin smooth or nearly smooth on forelimbs and smooth on sides of head and body and ventral surfaces. Head slightly wider between jaw articulations than between outer edges of upper eyelids; head usually narrower than body (especially in gravid females) or about as wide. Head width between angles of jaws 28–34% of SVL. Snout sloping, bluntly pointed or rounded in profile, truncately rounded (usually) or bluntly pointed in dorsal and ventral aspect. Nares situated near tip of snout, directed slightly posterolaterally; nares visible from front and from below but not from above. Canthus rostralis rounded; loreal region nearly vertical, slightly concave to flat. Interorbital distance wider than upper eyelid. Eye equal to or longer than snout length; distance from center of naris to eye 59–79% of eye length. Tympanum nearly half of eye size, concealed dorsally and posterodorsally.

Hand (fig. 3) moderately large, its length 23–28% of SVL and 71–91% of head width between angles of jaws. Relative lengths of *appressed* fingers $3 > 4 \approx 2 \approx 1$; fingers 1, 2, and 4 all approximately equal when appressed, with overlapping discs; appressed first finger varies from slightly shorter to slightly longer than second. Finger discs weakly to moderately expanded; third finger disc 1.2–1.8 times wider than distal end of
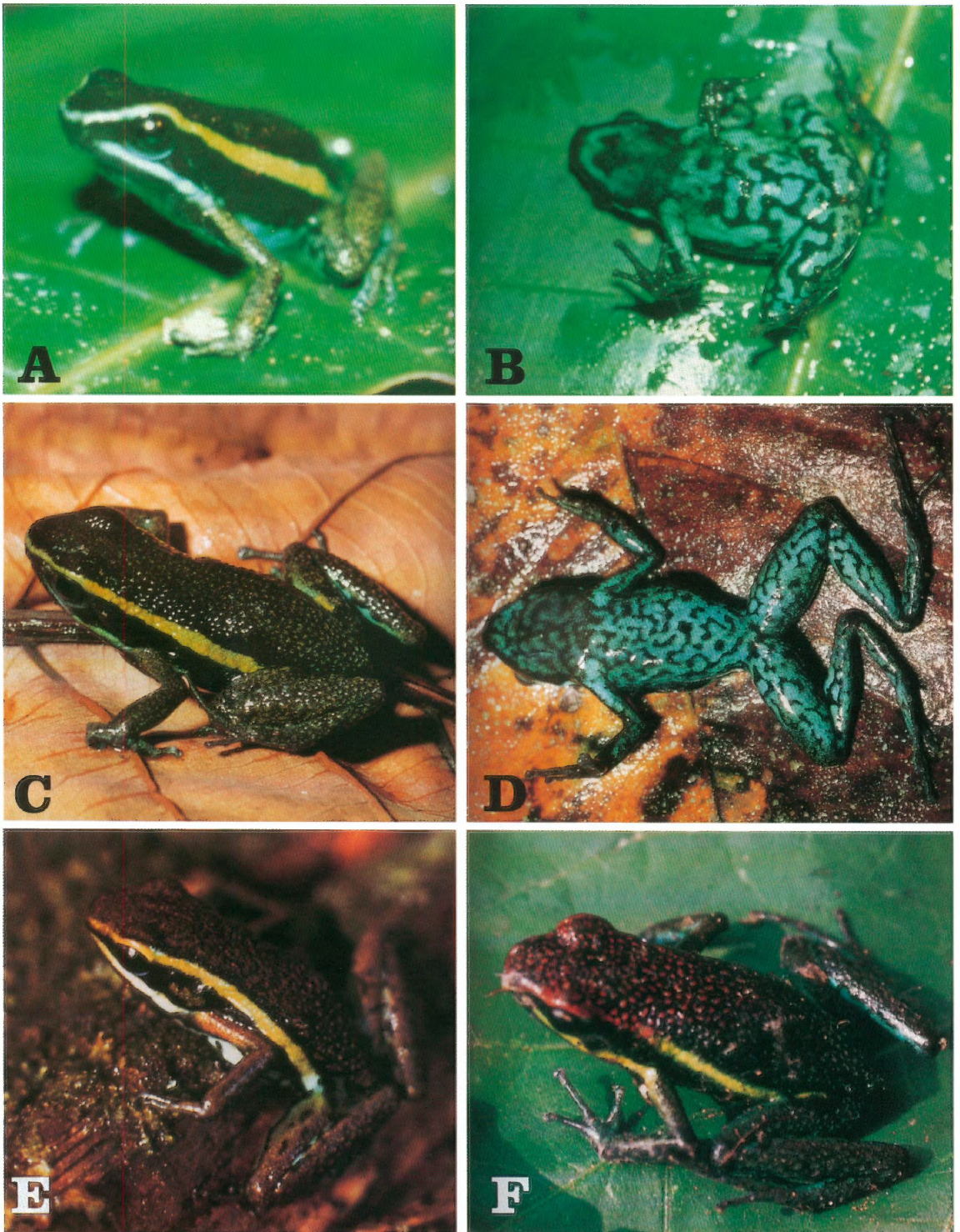
Fig. 1.   **A–D.** *Epipedobates simulans*, new species, in life. A, B. Lateral and ventral views of a paratopotype (AMNH 155164♂). C, D. Dorsal and ventral views of a paratype from Atalaya, Depto. Cusco (AMNH 155165♂). [From color transparencies by L. O. Rodríguez.]

E. *Epipedobates petersi* (Silverstone, 1976). View of holotype (USNM 166763) in life, from Río
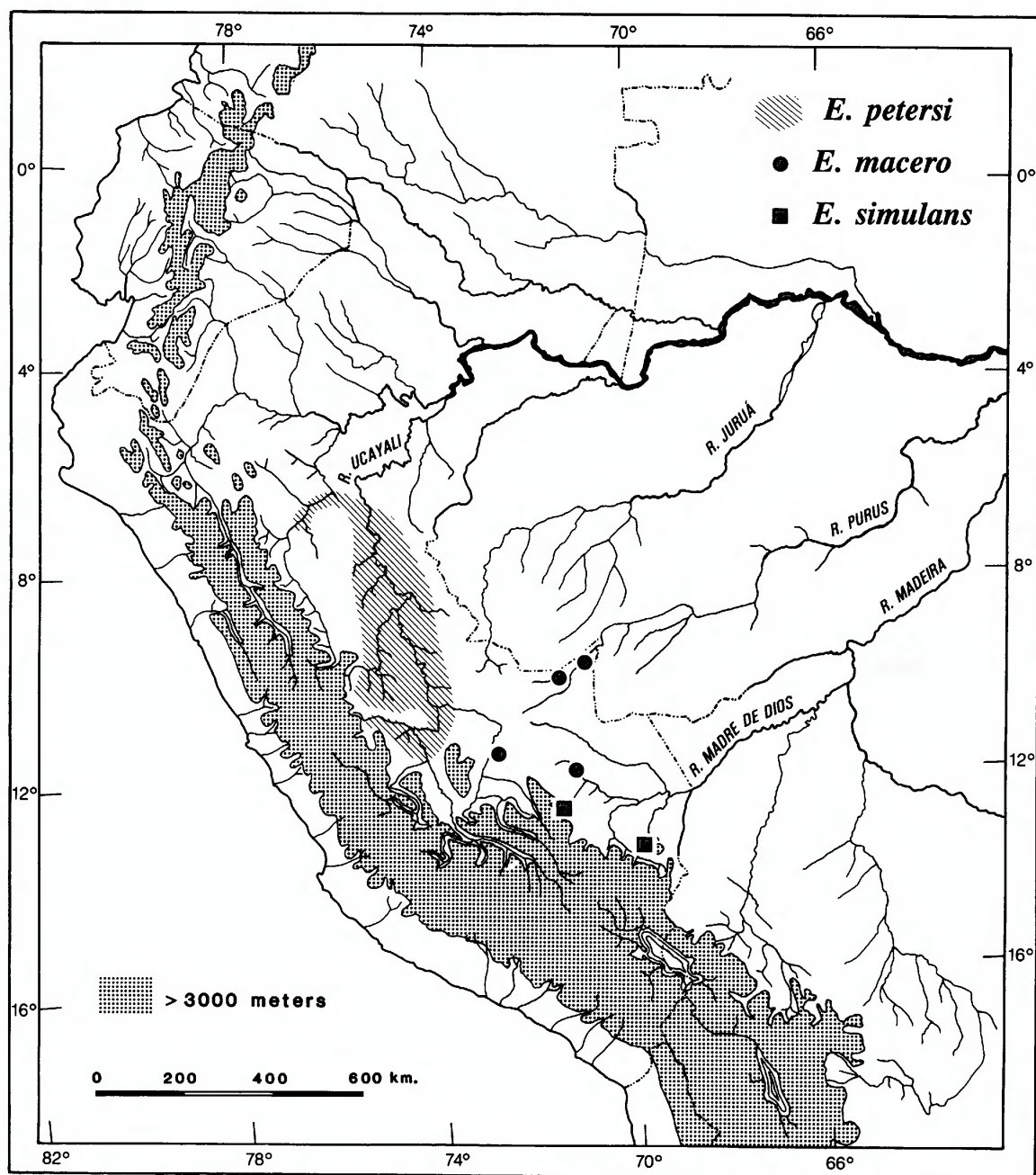
Fig. 2. Western Amazonia, showing localities for *Epipedobates simulans*, new species, and both new and previously published records for *E. macero* (see Remarks in text). Hatched area indicates distribution of *E. petersi* in the Río Ucayali and part of the Río Huallaga basins—based mainly on type specimens mapped and listed in Silverstone (1976: 19, 37).

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Nevati (Pachitea drainage), Depto. Pasco, Peru. [From color transparency made in July 1968, courtesy Asa C. Thoresen (see Silverstone, 1976, frontispiece 2, for color painting based on same transparency).]

F. *Epipedobates macero* Rodríguez and Myers. A specimen from Quebrada Esperancillo, near Puerto Esperanza, Río Alto Purús, Depto. Ucayali. [From color transparency by Patrick de Rham.]

TABLE 1
Size and Proportions of Adult *Epipedobates simulans*, New Species, in the Type Series

Character	N	Mean ± 1 SE	SD	CV (%)	Range
Snout-vent length (SVL) in mm	6♂	21.12 ± 0.49	1.21	5.74	18.9–22.4
	7♀	24.84 ± 0.51	1.34	5.38	23.6–27.0
Tibia length[a]/SVL	6♂	0.521 ± 0.011	0.026	5.04	0.47–0.55
	7♀	0.483 ± 0.009	0.023	4.75	0.45–0.51
Head width[b]/SVL	6♂	0.319 ± 0.006	0.014	4.39	0.30–0.34
	7♀	0.300 ± 0.006	0.015	4.89	0.28–0.32
Center naris to eye edge/eye length	6♂	0.737 ± 0.020	0.049	6.67	0.66–0.79
	7♀	0.680 ± 0.024	0.064	9.45	0.59–0.77
Hand length[c]/SVL	6♂	0.264 ± 0.006	0.015	5.81	0.24–0.28
	7♀	0.251 ± 0.005	0.014	5.64	0.23–0.27
Hand length/head width	6♂	0.829 ± 0.027	0.066	7.95	0.71–0.91
	7♀	0.838 ± 0.018	0.047	5.58	0.76–0.89
Width 3rd-finger disc/finger	6♂	1.406 ± 0.056	0.137	9.77	1.20–1.60
width below disc[d]	7♀	1.638 ± 0.052	0.138	8.43	1.40–1.80

[a] Tibia length is the shank measured from the heel to the convex surface of the knee (with limb segments flexed at right angles), roughly approximating the length of the tibiofibula.

[b] Greatest head width, measured between jaw articulations.

[c] Hand length measured from proximal edge of large medial palmar tubercle to tip of longest (3rd) finger.

[d] Digit width measured near distal end of penultimate phalanx.
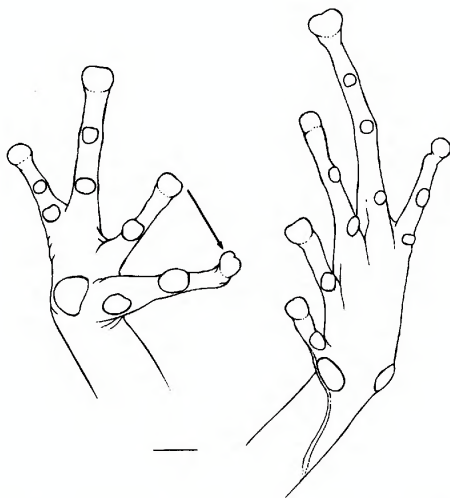

Fig. 3. Right hand and left foot of *Epipedobates simulans*, new species (MUSM 15505, ♂ paratype). Arrow indicates position of shorter digit when the first two fingers are appressed; finger 1 varies from slightly shorter than finger 2 to slightly longer (as in this specimen). Scale line = 1 mm.

adjacent phalanx—tending to be wider in females (table 1). A large outer metacarpal tubercle on base of palm and a smaller inner metacarpal tubercle on base of first finger, these being relatively low, with rounded surfaces. One subarticular tubercle on fingers 1, 2, and two subarticular tubercles on fingers 3, 4; subarticular tubercles well developed and prominently raised, although distal one on finger 3 and/or 4 sometimes weaker. No supernumerary tubercles. No outer metacarpal fold. Lateral finger keeling absent or weakly discernible only distally and on third finger of males. Finger 3 is sexually dimorphic, being somewhat wider in all six male paratypes (fig. 4).[6]

Hind limbs long, with heel of adpressed

[6] The taxonomic distribution of a widened or swollen third finger in dendrobatids has been puzzling, occurring in some *Epipedobates* and diverse *Colostethus*. Myers and Donnelly (1997: 24–25), recently suggested that it might be "another plesiomorphic trait that (like the various pale stripes) is variably expressed in dendrobatids."
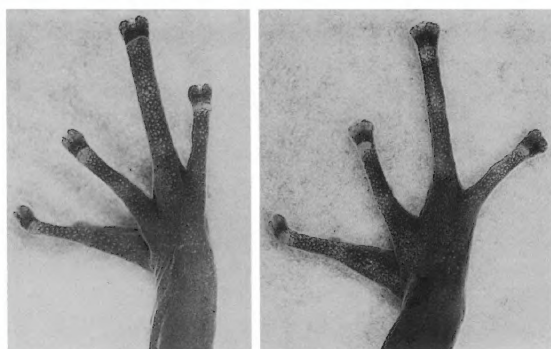
Fig. 4. Sexual dimorphism in third finger of adult *Epipedobates simulans*, new species. **Left.** Right hand of a male (AMNH 155164, 22 mm SVL), showing digit III slightly widened for its entire length, ×5.6. **Right.** Right hand of a female (MUSM 15504, 24 mm SVL), with digit III unmodified, ×5.2.

limb reaching to eye or between eye and tip of snout. Tibia 45–55% of SVL. Relative lengths of appressed toes 4 > 3 > 5 > 2 > 1; first toe usually reaching base of subarticular tubercle of second. No basal webbing or toe fringes (ventrolateral keeling very weak or absent), but some specimens (e.g., fig. 3) with a weak keel extending from free edge of first toe and along edge of inner metatarsal tubercle to tarsal fold; no outer metatarsal fold. Toes with moderately expanded discs about as wide or wider than finger discs (fig. 3). One to three moderately raised subarticular tubercles (one each on toes 1, 2, two each on 3, 5, and three on 4); no basal webbing. Two or sometimes three large metatarsal tubercles, with low, rounded surfaces; inner metatarsal tubercle slightly larger than outer metatarsal tubercle; a smaller median metatarsal tubercle, sometimes absent or faint, situated between and slightly proximal to the inner and outer tubercles. No supernumerary tubercles.

Distal half of tarsus with tarsal keel bearing a slightly raised tubercle at proximal end; ventrolateral side of tarsus relatively smooth, not especially rugose or tubercular.

COLOR PATTERN: In life (figs. 1A–D), the noticeably granular body is blackish with bronze highlighting middorsally, turning black dorsolaterally. The flanks are black, with a distinct yellow or greenish yellow stripe that extends obliquely from the groin to

above the eye and forward along the canthus rostralis to join its mate around the snout; this stripe may become paler, even whitish, anterior to the eye (but was noted as being yellow on snout of holotype). A pale blue or greenish blue labial stripe commences between naris and eye and extends posteriorly under eye and tympanum to the base of the upper arm. A bright yellow spot on anterodorsal base of thigh above groin, mostly concealed with limbs at rest (barely visible on right thigh in fig. 1C); there is no calf spot and no pale markings in axilla or groin. The limbs are bronzy brown with green and black suffusions. The ventral surfaces are overall blue with variable black reticulation; throat suffused with dark gray.

In preservative, the dorsal and lateral surfaces are faded brown (in the three old BMNH specimens) or blackish (in the more recent material), with the oblique lateral stripe and proximal thigh spot having faded from yellow to gray. The anterior extension of the lateral stripe becomes obscure on the canthus rostralis; the thigh spot varies in distinctness but never has sharply defined edges. The upper lips are brownish or blackish; the pale labial line (always with ill-defined edges) varies from obscure (especially anteriorly) to being readily evident on the dark ground from nostril or from anterior edge of eye to the arm. Ventrally, the black reticulation has faded to brown (in the BMNH specimens) or blackish gray on a tan or brown ground; the original ventral pattern is very obscure in most specimens.

OSTEOLOGY

Maxillary teeth are present, as confirmed for all specimens in the type series.

Additional data are obtainable from an X-ray photograph of MUSM 15504 (fig. 5): The skull is nearly as wide as long. Frontoparietals in medial contact throughout. Sphenethmoid in close contact with anterior ends of frontoparietals. Small teeth present on maxillae and premaxillae. Mandible with a pronounced retroarticular process. Eight presacral vertebrae, with no obvious fusions; sacral diapophyses barely dilated. Phalangeal formula of hands 2-2-3-3, of feet 2-2/1-3-4-3. Each digit with a short, prominently T-
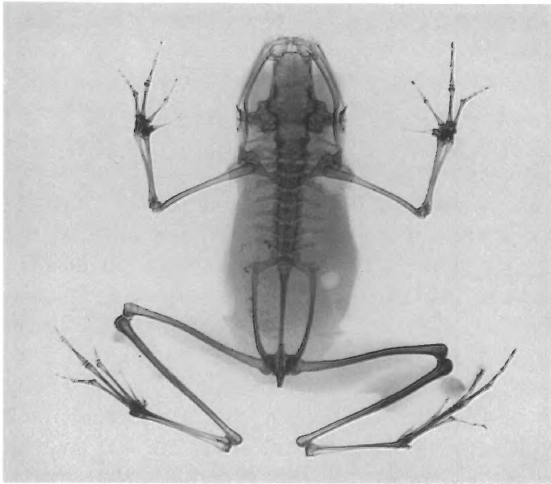
Fig. 5. *Epipedobates simulans*, new species. Radiograph of an adult female (MUSM 15504), ×1.8.

shaped terminal phalanx, with the transverse process lying at about the middle of the fleshy disc.

MYOLOGY

Minimal dissection of one specimen of *Epipedobates simulans* (AMNH 155166) showed jaw and thigh musculature more or less typical of dendrobatids and especially similar to that of *E. macero* (Rodríguez and Myers, 1993: 7). The flesh is weakly pigmented superficially, probably appearing light gray in a fresh carcass.

The massive superficial slip of the m. depressor mandibulae originates from the dorsal fascia and overlaps the posterodorsal margin of the tympanum. A largely concealed, deeper slip of this muscle originates dorsally from the otic ramus of the squamosal and anteriorly from the posterior margin of the tympanic ring.

There is no m. adductor mandibulae externus superficialis. The mandibular branch of the trigeminal nerve laterally crosses the deeper m. adductor mandibulae posterior subexternus, which originates from the abbreviated zygomatic ramus and anterior edge of the squamosal and, perhaps (?), partly from the anteromedial part of the tympanic ring, which closely overlies the posterior part of the adductor.

On the thigh, the tendon of the deep m.

semitendinosus pierces the edge of the distal tendinous end of the m. gracilis complex prior to insertion.

VOCALIZATION

The advertisement call of *Epipedobates simulans* is a long train of uniform notes that are heard as short, high-pitched "peeps," which are well-spaced, being mostly given at a rate of about 2 notes per second (figs. 6–8). One 61-sec section of tape contains 66 notes for an overall rate of 1.1 notes/sec, but there are 2 notes/sec in shorter sections of this long call.

The notes are short ($\approx$ 0.07–0.11 sec) and narrowly tuned, with pronounced frequency modulation. Each note is initiated at about 3800 or 4000 Hz and rises sharply some 500–600 Hz. Frequency seems to be constant within a note train, with only minor variation (e.g., third note in fig. 6B). However, there is clear individual variation in the frequencies at which notes are initiated and terminated. This is indicated in the figured spectrograms, especially figure 8, which shows alternating notes of two frogs simultaneously recorded at the same locality.

Notes are variably pulsed, with complex intracall and individual or possibly interpopulational diversity. Waveforms of several calls from the upper Río Tambopata basin show usually strongly pulsatile notes with very irregular amplitude modulation (figs. 6, 8, 9A–G). In contrast, one recording from the locality Atalaya shows more uniformly shaped waveforms with little amplitude modulation (fig. 7); these notes are rapidly pulsed at beginning and end (fig. 9H).

The preceding description is given in the absence of temperature data, although some measurable temperature-correlated variation is likely to exist. For example, note repetition rate is likely to show a positive correlation with temperature, whereas note duration might be expected to be negatively correlated.

NATURAL HISTORY

Epipedobates simulans is a diurnal inhabitant of the forest floor, at the limit between the montane forest and the lowlands (400–600 m) in southeastern Peru. The holotype

was found at night (1930 h) sleeping on a leaf 10 cm aboveground. A few nights later, an adult male similarly was found sleeping on a leaf aboveground. In wet tropical forest, such sleeping behavior is not uncommon among small, diurnal terrestrial frogs, including other species of *Epipedobates*.

In the region of the type locality, the lower ridges along the Río Távara run parallel to the Andes and seem to be of Tertiary origin. Conditions are humid (although other low Andean localities at more northern latitudes are even more humid). Higher parts of the ridges are less steep and, with increasing elevation, fog becomes frequent and tree trunks become covered with moss.

Forest at the type locality is about 30–35 m tall, with some emergent trees reaching 40–45 m. The vegetation composition is highly diverse (197 spp./ha, >2.5 cm dbh), variable, and mixed, on quartzite-based and regular clay soils. Common plants include species of *Hevea, Hernandina, Calophyllum, Qualea, Inga, Iriartea, Brosium, Otoba, Geonoma, Pourouma, Tococa*, and emergent trees such as *Dypterix, Cedrelinga, Cedrela*, and *Buchenevia*, as well as tree ferns, orchids, and species of Rubiaceae, Myrtaceae, Marantaceae, etc. Most are lowland plants found here at "unusually" high elevation, although there is a set of taxa different from those in the lowlands and represented only at these elevations. *Epipedobates simulans* is a part of this rich, complex biota.

COMPARISONS WITH *E. PETERSI*

SIZE: *Epipedobates petersi* is a larger frog on average. Measurements of 15 paratypes in the American Museum collection gives the following snout-vent lengths (SVL in mm) for adult *E. petersi*:

6 ♂: $\bar{x}$ = 25.50 ± 0.39, SD = 0.96 (24.6–27.0)
9 ♀: $\bar{x}$ = 27.46 ± 0.74, SD = 2.22 (24.4–30.3)

In contrast, average SVL for adult *E. simulans* is about 21 mm for males and 25 mm for females (table 1).

COLORATION: Color patterns are essentially identical. The dorsum of *E. simulans* (fig. 1C), however, seems to be darker than in *E.*

petersi (fig. 1E). The back is essentially brown in *petersi*; in *simulans* it is basically black but with a middorsal highlighting of bronzy brown color atop the rough skin granules. However, we know nothing about extent of variation in this character.

The size and color differences are suggestive of different species but do not provide conclusive evidence. Silverstone (1976) had fewer specimens and can not be faulted for including a few *simulans* among his paratypes of *petersi*. Call differences, however, provide convincing evidence that *E. petersi* sensu Silverstone is a composite of at least two species.

VOCALIZATION: Icochea recorded *Epipedobates petersi* in October 1993 in Yanacha-ga-Chemillen National Park (Depto. Pasco). A frog calling in concealment was identified as *E. petersi* after the recording was made.[7] It is a long call, with one recorded segment being 175 sec before significant faltering. It is a rippling train of rising and falling notes given either singly or grouped (usually paired). The notes are pulsatile with variable amplitude modulation (waveforms, fig. 10). Duration in a sample of notes from calls used for figures 10–11 averages 0.055 sec (0.04–0.07 sec, N = 51) as determined by time-cursor measurement of waveforms; when arranged in pairs, the internote interval for couplets averages 0.093 sec (0.08–0.11 sec, N = 17) and the time between couplets is 0.258 sec (0.23–0.29 sec, N = 10).

The rippling effect produced by varying emphasis of individual notes can be visualized by differences in waveform amplitude and intensity of the spectrographic tracings (fig. 10A, B). When paired, as in figure 10, one couplet may be softer or louder than another couplet, or either note of a couplet may be louder than its mate. One might imagine that such an effect also could be produced if the unseen frog being recorded were slowly circling away from and then toward the mi-

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[7] The call of a second species of unidentified frog (probably *Leptodactylus*) on the tape is readily distinguished from the call attributed to *E. petersi*. It is a steady train of short whistles weakly modulated at a much lower frequency—2280–2640 Hz, suggesting a larger species of frog. Occasional notes also are given in isolation in the background of the *Epipedobates* calls (fig. 10).
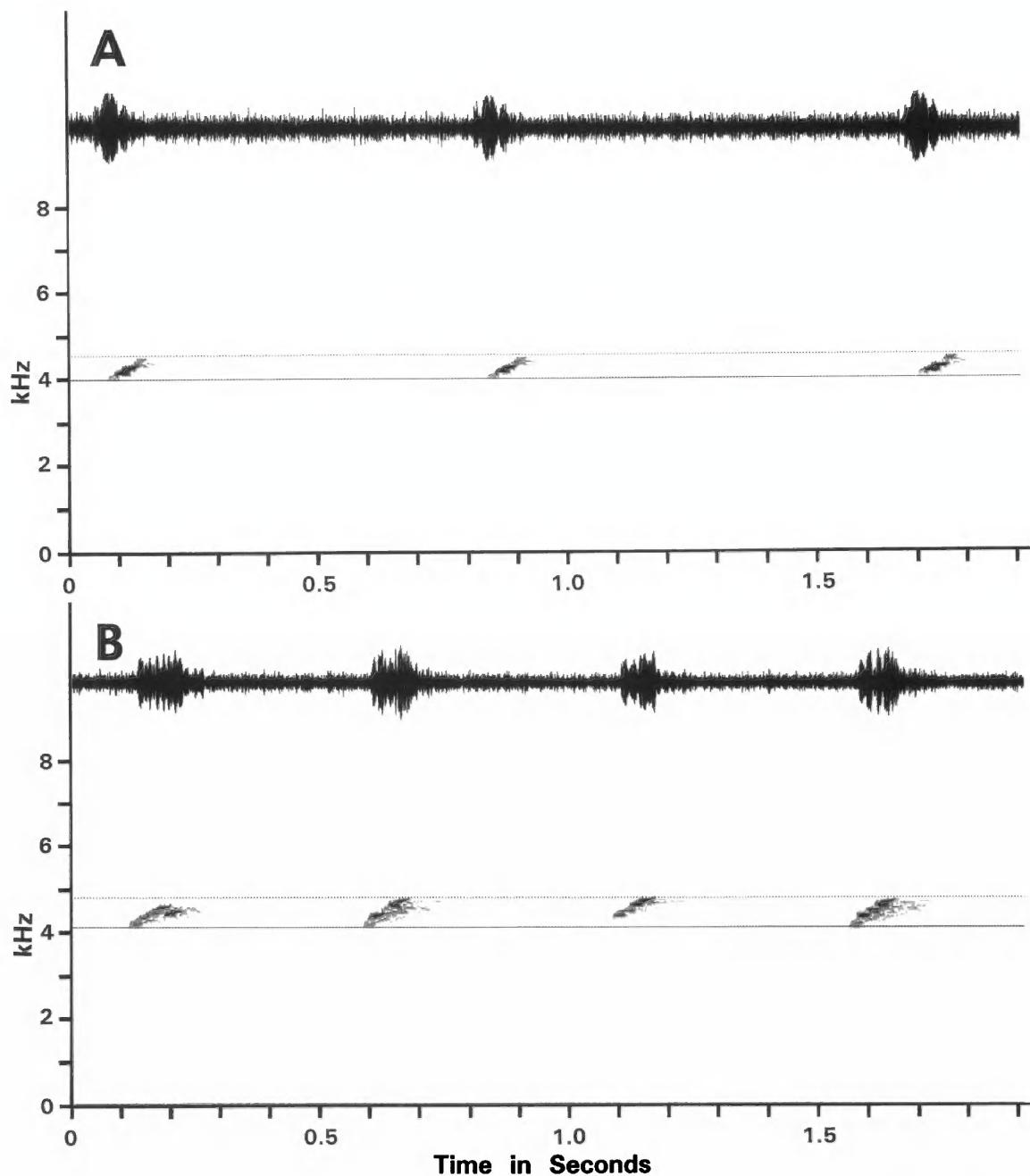
Fig. 6.   Advertisement calls of two individuals of *Epipedobates simulans* from ridge along Río Tá-vara (vicinity of type locality), Depto. Puno, shown as narrow-band (59 Hz) spectrograms, with matching waveforms. **A.** From 550 m elevation. Frequency cursors set at 4000 and 4560 Hz. **B.** A faster call from a site below 500 m elevation. Frequency cursors at 4120 and 4800 Hz. Both recorded by L. O. Rodríguez, June 3, 1992, temperatures not noted (AMNH herpetology reel 268).
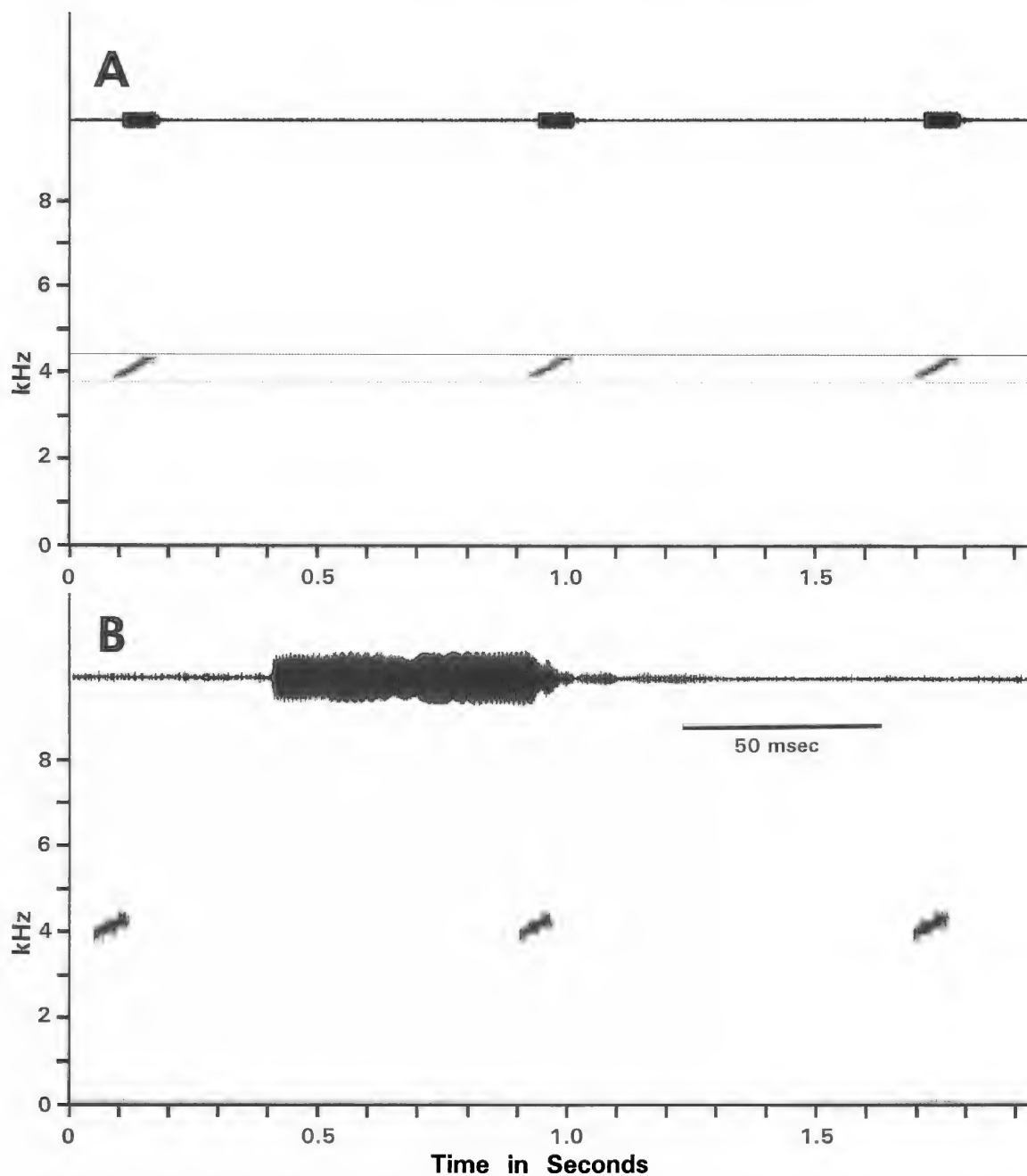
Fig. 7.   Advertisement call of *Epipedobates simulans* from Atalaya, 600 m, Depto. Cusco. **A.** Narrow-band (59 Hz) spectrogram and matching waveforms. Frequency cursors set at 3760 and 4400 Hz. **B.** Same notes graphed wide-band (300 Hz), with expanded waveform of first note on left. Recorded by L. O. Rodríguez, August 28, 1993, temperatures not noted (AMNH herpetology reel 272).
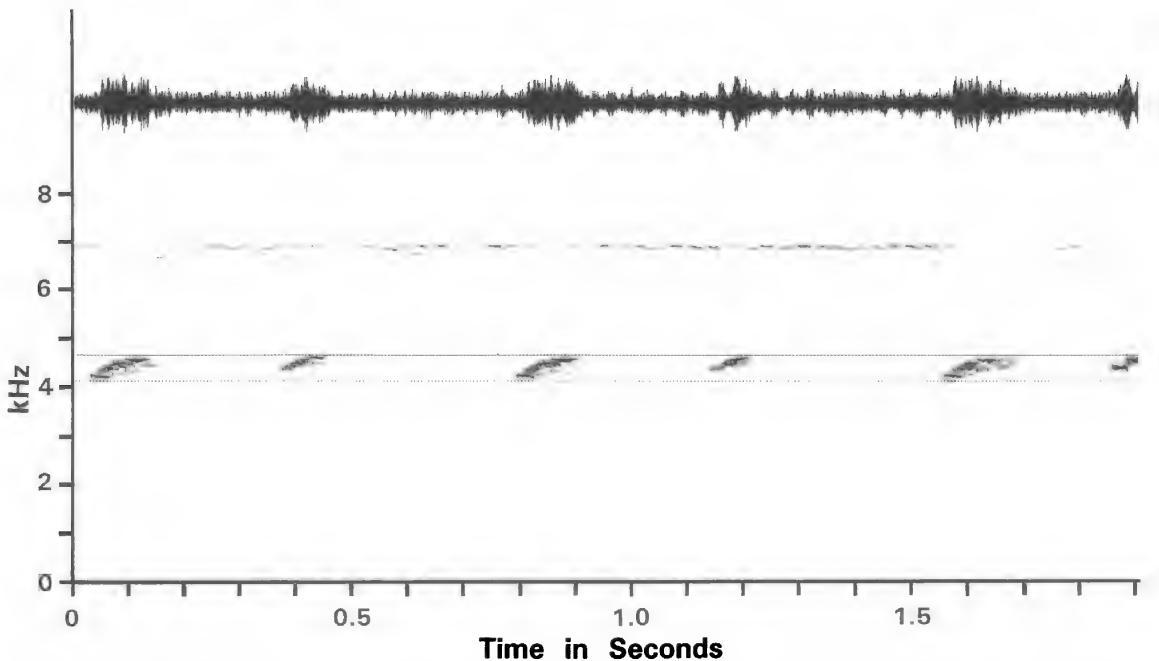
Fig. 8. Alternating notes from two calling *Epipedobates simulans*, recorded at same site as spectrogram in figure 6B. These two frogs were calling at slightly different frequencies—the first at 4120–4600 Hz and the second at 4320–4640 Hz. Guide cursors are set at 4120 and 4640 Hz. Recording data as in figure 6.

crophone. But the rippling is constant in some 5 minutes of tape time and is heard also in the recording of a frog calling in a terrarium.

A shift from a train of single notes to a train of paired notes (couplets) occurs within single calls, as shown in figure 11. The train of single notes may be interrupted by a couplet (fig. 11B), or odd groups of three (fig. 12B) or four notes (fig. 11E) may be inserted among the couplets; internote spacing causes at least the first two notes in the larger groups to resemble a normal couplet. Frequency seems relatively constant except that the call may start off at a lower frequency (fig. 11A).

Schlüter (1980: 154–155) described the call of *Epipedobates petersi* as comprising nonuniformly grouped notes in the Panguana region (Río Pachitea, Ucayali drainage).[8] Schulte (1989: 44), however, stated that *Epipedobates petersi* also has a much longer call, exceeding 30 sec and comprising single (ungrouped) notes. Both authors are correct,

as shown by variation within a single calling sequence, as described above and demonstrated in figure 11.

At first glance, Schlüter's (1980: 154) sound spectrogram of *E. petersi* looks quite different from those in figures 9–10, but the recording on his original tape was overloaded, as frequently happens.[9] His original spectrograph, reproduced here as figure 12A, shows a grouping of seven notes in about 1.3 sec—the call starts with a close grouping of two contiguous notes followed in about 0.05 sec by a single note, then, at intervals of nearly 0.1 sec, two groups of contiguous paired notes. Nearly identical sequences of

[8] Schlüter (1987: 19) later published a color photograph of an adult *E. petersi* from the same area.

[9] Other "good" examples of spectrograms produced from overloaded recordings can be seen in Myers and Daly, 1976, especially fig. 17). Those of us who have carefully followed printed instructions for adjusting the VU meter of tape recorders eventually learn that a lighter touch is required for many frog voices. As one recordist put it: "It took me quite a while, and many ruined recordings, to realize that a high-pitched, high volume call overloads the tape unless the VU recording level peaks at no more than about one-third of the distance to the red line, preferably less" (R. G. Zweifel, in litt., 12/97).
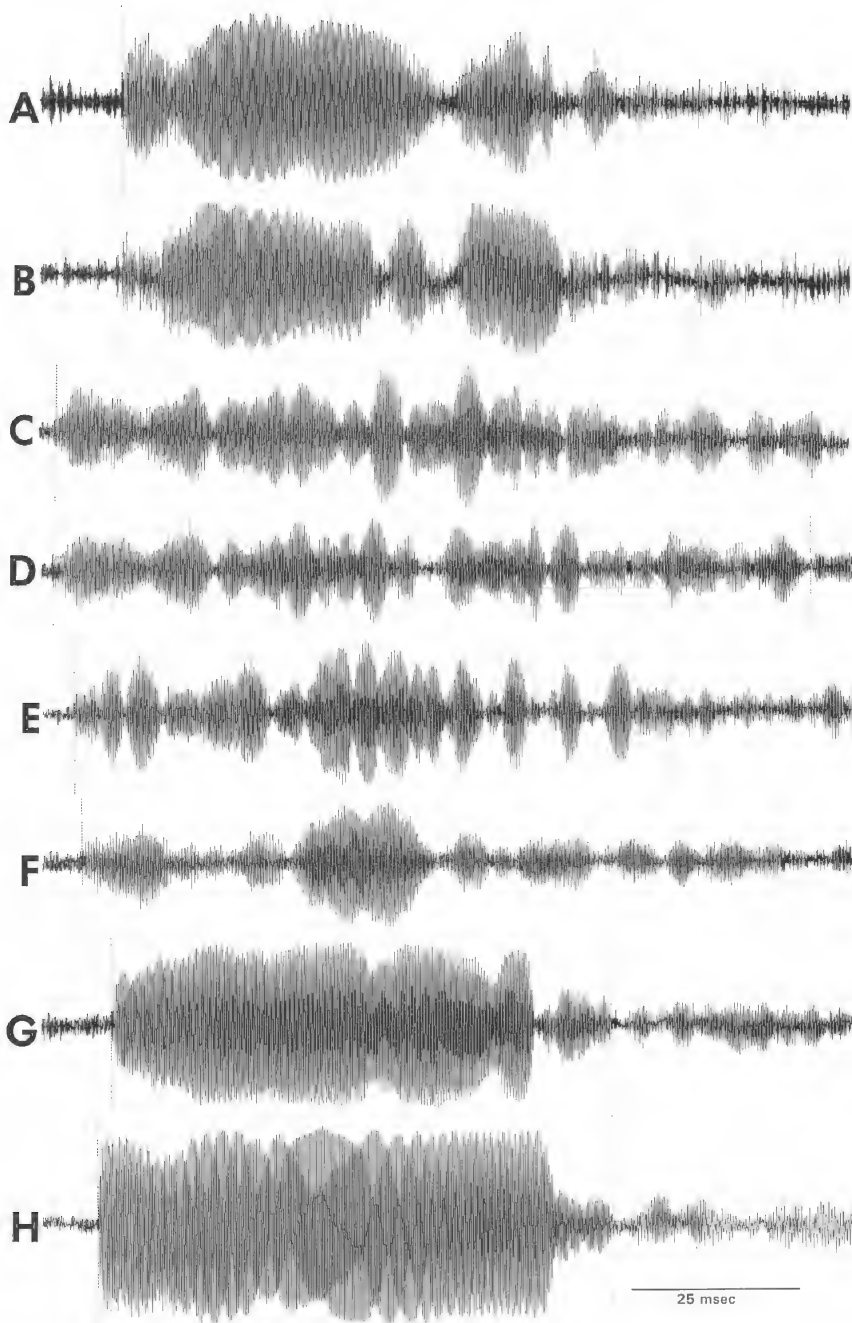
Fig. 9. Expanded waveforms showing variable amplitude modulation of pulses in advertisement calls of *Epipedobates simulans*, new species. **A, B.** Notes from same recording used in figure 6A. **C–G.** Notes from recording used in 6B. **H.** Representative note from recording used in figure 7. Notes are initiated rather abruptly, but endings are less precise owing to terminal drag. Time cursors approximate the duration of each note as follows: 0.074 sec (A), 0.085 sec (B), 0.114 sec (C), 0.112 sec (D), 0.088 sec (E), 0.104 sec (F), 0.074 sec (G), 0.076 sec (H).
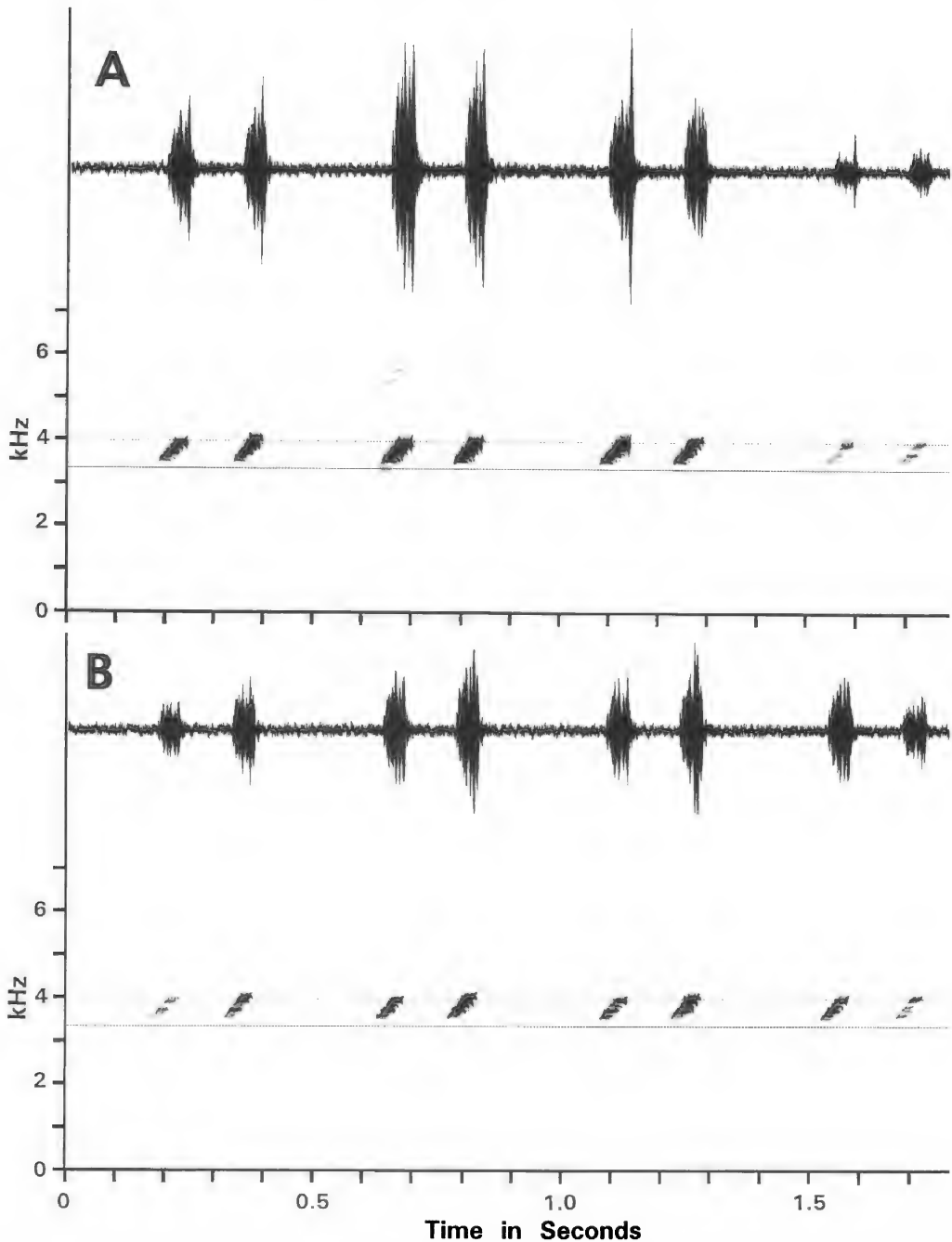
Fig. 10. Advertisement call of *Epipedobates petersi* from Estación Paujil, Parque Nacional Yana-chaga-Chemillen, Depto. Pasco, Peru. Two segments from a 47-sec recording, shown as narrow-band (59 Hz) spectrograms with matching waveforms. Frequency cursors in each segment are set at 3320 and 3960 Hz. Recorded by J. Icochea, October 21, 1993, 0622 hours, temperature 23°C (copy on AMNH herpetology reel 279).

Differences in waveform amplitude and intensity of spectrographic tracings reflect internote differences in loudness, which are clearly evident to the human ear (faint harmonics above the loudest two couplets in A are machine artifacts caused by signal overload). Notes in a couplet may be almost uniformly stressed, whether loudly or softly, or either the first or (usually) the second note of a pair may be distinctly louder. See figures 11 and 12 for other variation.
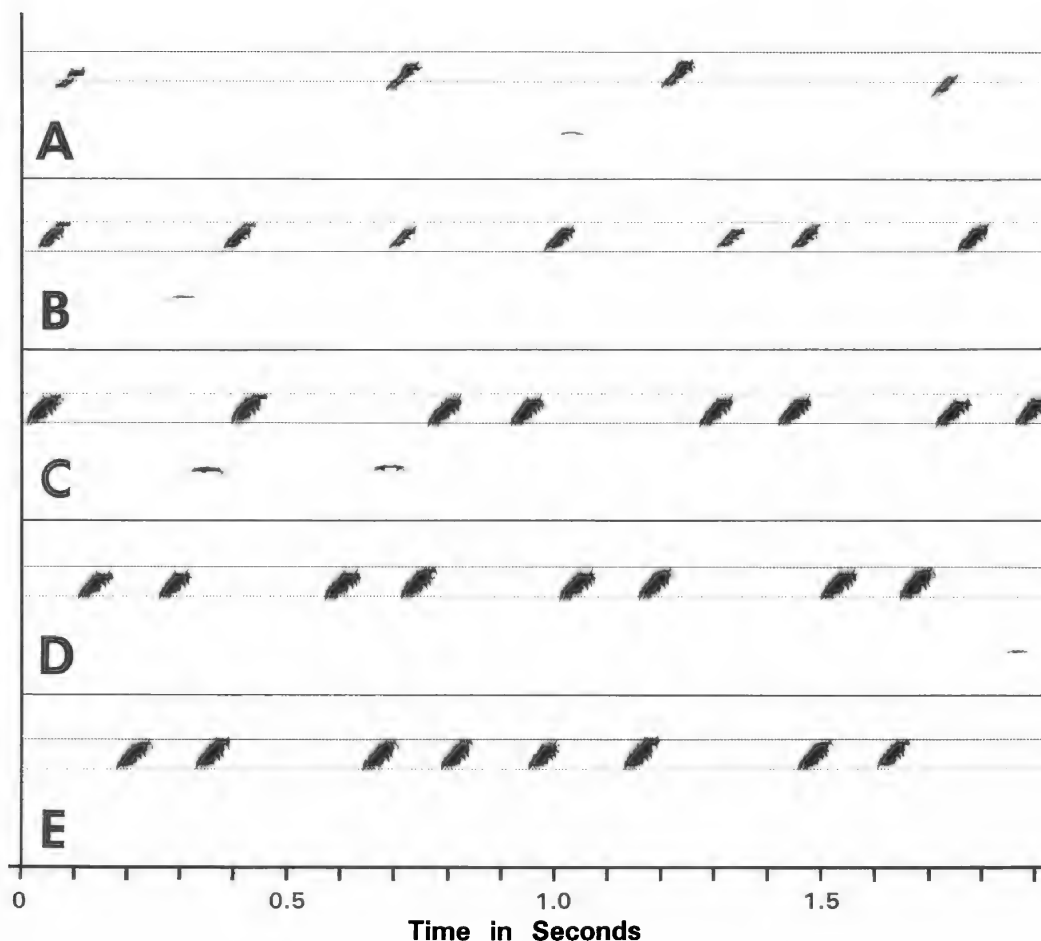
Fig. 11.   Intracall variation in vocalization of *Epipedobates petersi*, showing, in chronological order, five segments selected from a 175-sec recording. Narrow-band (59 Hz) spectrograms with frequency cursors set at 3320 and 3960 Hz. Occasional lower notes (at about 2200–2400 Hz) are of an unidentified frog calling in background. (Recording data as in fig. 10).
A. Beginning of call (excluding first note), consisting of single notes. **B.** Part of a continuing train of single notes, with one couplet inserted. **C.** Shift from the train of mostly single notes to a train of couplets (paired notes). **D.** Continuing train of couplets. **E.** A group of four notes inserted in the train of couplets.

notes are found in our recording (e.g., fig. 12B), with the first three notes possibly representing a couplet plus a single note (the internote interval is 0.09 sec between the first two notes and 0.11 sec between the second and third notes).

After the above comparison was made, Dr. Schlüter generously provided his 20-year-old recording for reanalysis by more sophisticated instrumentation than was available in 1980. Video spectrographic scrolling of this old recording shows trains of both couplets *and* triplets, as well as isolated single notes

and groups of four notes. One 25-sec segment of tape contains an unbroken sequence of 45 triplets, which predominate over shorter trains of couplets. A triplet of notes therefore is not merely an anomalous grouping in a train of either single notes or couplets, but can be maintained as a constant call for many seconds. The rippling effect caused by uneven emphasis given individual notes is heard through this recording (although not evident spectrographically, presumably because of overload). The spectrograms in figure 13 show partial sequences both of cou-
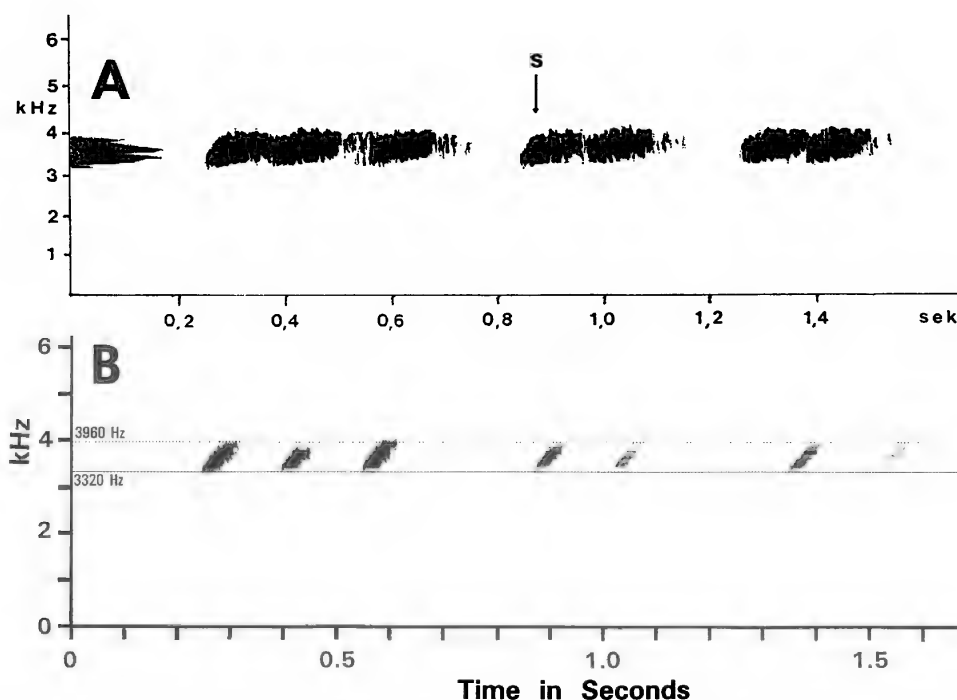
Fig. 12. **A.** An old sound spectrogram of *Epipedobates petersi*, reproduced from Schlüter (1980: 150) [from a 1978 recording, data in fig. 13 caption]. **B.** A similar arrangement of notes selected from the 47-sec recording of figure 10.

The spectrogram in A was produced from an overloaded recording, apparently with wide-band filter (compare fig. 13). Despite closeness of the notes (caused by drag induced by overloading), a triplet of notes (or a couplet + 1) followed by two couplets can be visualized. The timing of the "triplet" and first couplet are nearly the same in A and B.

plets and triplets plus one group of four notes.[10] These notes are distinctly pulsed albeit with variable amplitude modulation (fig. 14).

The variability of note spacing and the rippling of sound in the call of *Epipedobates petersi* is very different from the continuous trains of single, uniformly spaced notes in *E. macero* and *E. simulans*. *Epipedobates macero* calls at about the same frequency as *petersi*, but the very short notes are not frequency modulated and are closely spaced, with about 10 notes/sec (Rodríguez and Myers, 1993: 8–9). The call of *E. simulans* differs from both in that the notes are more widely spaced (1–2 notes/sec) and produced in a higher frequency range (mostly or entirely above 4000 Hz).

REMARKS

As presently known, *Epipedobates simulans* occurs at localities about 170 km apart (northwest to southeast) in lower montane Andean forest in the upper Río Madre de Dios watershed. The localities are in the adjacent conservation-priority zones 13 (Manu) and 14 (Tambopata) as mapped by Rodríguez (1996). *E. simulans* therefore occurs well south of the range of *E. petersi*, which occupies the Río Ucayali and nearby Río Huallaga basins (fig. 2, and Silverstone, 1976: fig. 16).

Duellman and Thomas (1996: 6) erred in extending the range of *E. petersi* eastward out of the Ucayali watershed to Balta in the drainage of the Río Alto Purús, near the Brazilian border. At first glance, the record does

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[10] The question then arises—can quadruple notes also be repeated in trains? However, this may be asking too much of the poor frog. As it is, no other dendrobatid is known to produce trains of single, double, or triple notes, not to mention the occasional group of four.
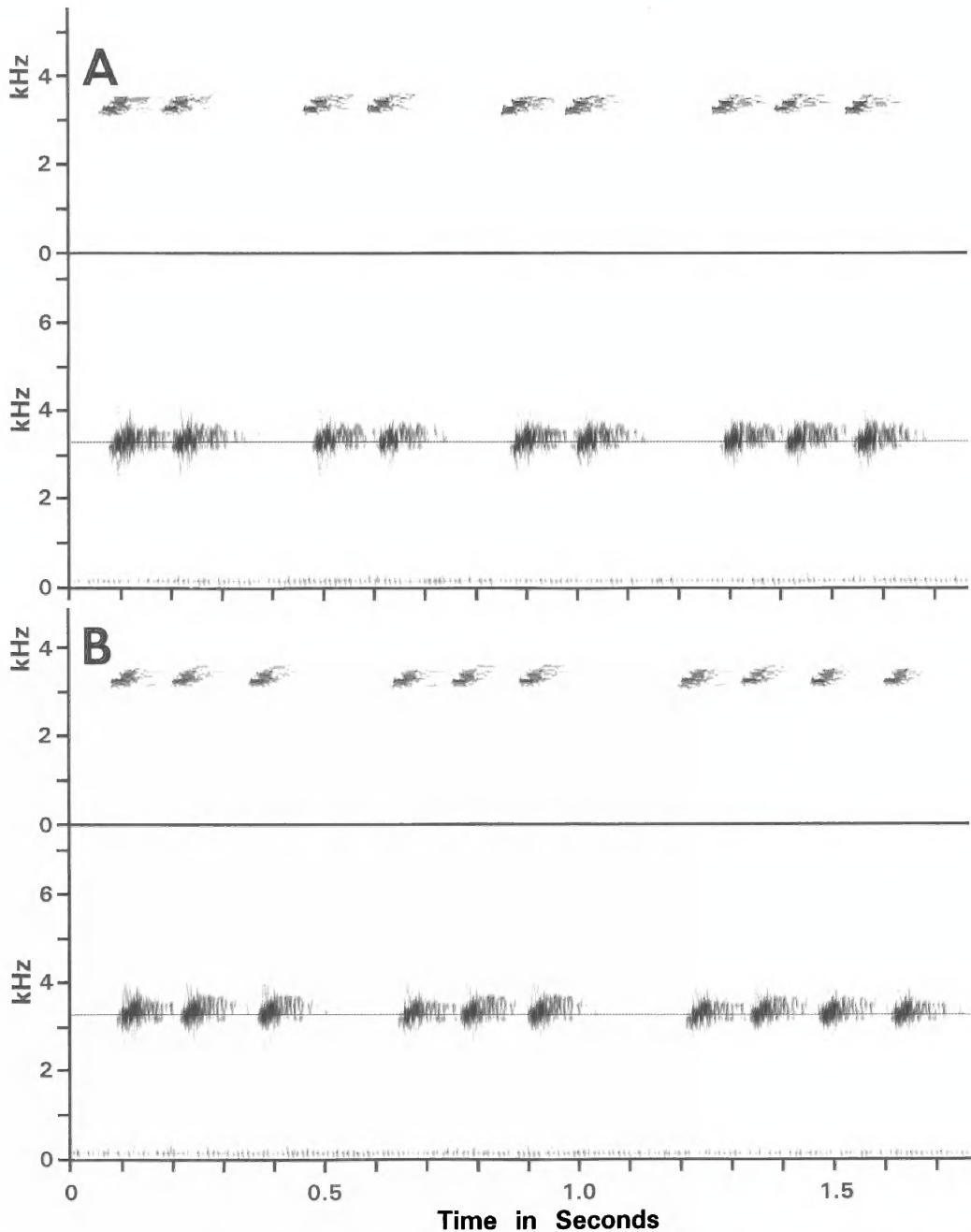
Fig. 13.   Advertisement call of *Epipedobates petersi* from "Fundo Flor," west side Río Pachitea, about 6–8 km (airline) south of Panguana, Depto. Huánuco, Peru. Recorded by Andreas Schlüter in 1978, from frog in terrarium, air temperature about 23°C (copy on AMNH herpetology reel 279).

A, B. Two sets of narrow-band (59 Hz, upper) versus wide-band (300 Hz, lower) sound spectrograms from the same 20-year-old tape recording used for figure 12A. Reanalyzed on a Kay 5500 DSP Sona-Graph, with input setting of 34 dB, and display settings of 30 dB dynamic range and 15 dB analysis attenuation. Separation of the individual notes is achieved at these settings, but the overloaded nature of the recording remains evident. Frequency cursor set at 3320 Hz.
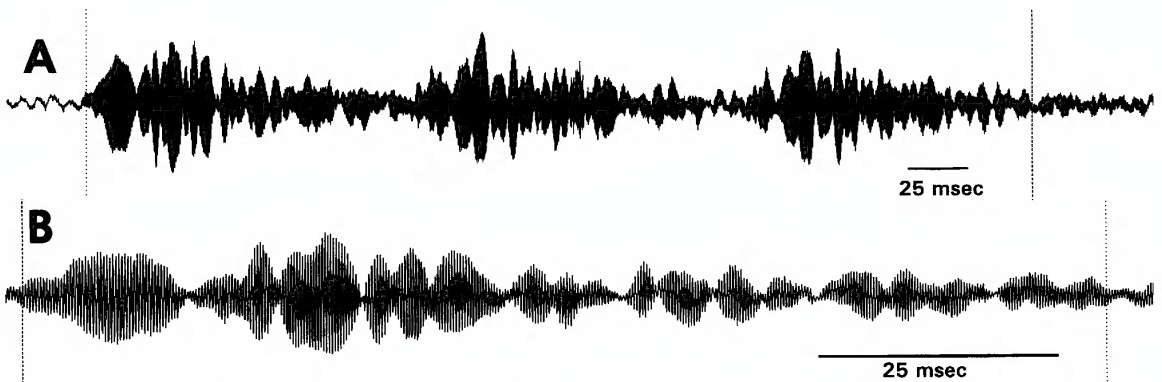
Fig. 14. Waveforms showing variation in amplitude modulation of pulses in *Epipedobates petersi*. A. Expanded waveforms of a triplet of notes; time between cursors = 0.393 sec. B. Further expansion of first note in above triplet; time between cursors = 0.113 sec. Data as in figure 13.

not seem improbable, but their description of a red-headed frog sounds unlike *E. petersi*. Their record seems to be based on *E. macero*, as supported by examination of other specimens (AMNH field series 11557, 11560) collected downriver, about 60 km northeast of Balta at Quebrada Esperancillo, Río Alto Purús (figs. 1F, 2).

This new Alto Purús record for *Epipedobates macero* is about 240 km north-northeast of the type locality on the Río Manu (upper Madre de Dios drainage), and some 300 km northeast of the Río Camisea (tributary of Río Urubamba, upper Ucayali drainage), where *E. macero* was recently reported by Morales (1996).

Epipedobates macero differs from *E. petersi* and *E. simulans* in being red over the head and at least the anterior dorsum, and in having an incomplete oblique lateral stripe (fig. 1F and Rodríguez and Myers, 1993: fig. 1). The oblique lateral stripe anteriorly terminates in the shoulder region of *macero* but extends forward above the eye in *petersi* and *simulans*; this difference is especially obvious in life, but it also serves to differentiate preserved specimens.

The defensive skin secretions of *Epipedobates simulans* have not been analyzed, but can be predicted to contain a variety of alkaloids, including histrionicotoxins and decahydroquinolines such as found in the skins of *E. petersi* and *E. macero* (Daly et al., 1987: 1082; Rodriguez and Myers, 1993: 8, 13–14). The presence of alkaloid uptake systems is supportive of some supraspecific

groupings, but alkaloid profiles from *Epipedobates* skin do not seem useful in supporting species distinctions. It is becoming clear that at least some dendrobatid alkaloids are sequestered from dietary sources; current knowledge, including systematic implications, were reviewed by Myers et al. (1995: 13–17) and Daly et al. (1997).

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Clarke arranged the loan of several old specimens (paratypes of *E. petersi*) that proved to represent the new species, from the British Museum (Natural History), London (BMNH).

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